

# THE ANNALS

AND

## MAGAZINE OF NATURAL HISTORY.

[FOURTH SERIES.]

No. 92. AUGUST 1875.

VIII.—*On the Position of Sagitta, and on the Convergence of Types by Pelagic Life.* By M. A. GIARD\*.

No animal has been more frequently shifted from one systematic division to another than *Sagitta*. Some have regarded it as a degraded vertebrate, and have placed it beside *Amphioxus*; others have considered it a heteropod mollusk; Oscar Schmidt declares that it "is neither a true annelid nor a legitimate mollusk"†; Leuckart, Schneider, and Claus approximate it to the Nematodea.

Häckel, in his 'Generelle Morphologie,' also places the Chætognatha among the Nematelmintha, and, further, he takes up the idea of Meissner with regard to the relationship of *Sagitta* and the Vertebrata. If we make a perpendicular section of the tail of a fish, we see clearly, he says, that the trunk of a vertebrate is formed originally of four antimeras, and not of two. The primitive form of the lower Vertebrata, like that of the Nematodea, is the *eutetrapleural interradiial* form. Thus we may put forth, with some appearance of reason, the hypothesis that the Vertebrata have issued from the Chætognatha by a progressive metamorphosis, whilst the Nematodea have been produced from them by a retrograde metamorphosis.

Since the admirable researches of Kowalevsky upon the

\* Translated by W. S. Dallas, F.L.S., from an article in the 'Revue des Sciences Naturelles,' tome iii. March 1875, communicated by the Author.

† The Doctrine of Descent and Darwinism, p. 37.

embryogeny of the *Ascidia*, Hæckel has modified his opinions upon this point: but we may say that the *Sagittæ* were a badly chosen group among the *Nematoidea* for the support of this theory; for we do not find in them the four muscular bundles mentioned by Hæckel, and their body is formed rather of two antimera.

On the other hand, the four primitive antimera occur with wonderful distinctness in the tail of the larvæ of certain *Ascidia* (*Perophora Listeri*); and even in some adult *Ascidia* they are clearly indicated by the quaternary symmetry of the buccal aperture.

Kowalevsky has himself expressed his opinion as to the position of *Sagitta* in the animal tree: he does not hesitate to place the *Chætognatha* among the true *Annelides*\*.

Before examining these various opinions more closely, it seems necessary to enter upon some general considerations which will enable us the better to appreciate the causes of their divergence.

One of the most difficult problems of modern zoology, and indeed that which must now-a-days preoccupy every thinking naturalist, is to determine in every peculiar arrangement of an organism what belongs to heredity, and what must be attributed to adaptation. Such inquiries present immense difficulties, and can only be fruitfully attempted with groups of which the embryogeny is sufficiently known. I speak, of course, of stratological embryogeny, which only dates from ten years back, and the general importance of which is unfortunately not understood by all who are engaged in zoological investigation. Every anatomical investigation that is not made with the object of elucidating this new embryogeny, is a work which may certainly possess some interest, but one which is no longer of our epoch, and even loses an enormous portion of its value. However, all naturalists of any merit have always been sustained in their efforts by a philosophical idea; and, although I may thereby subject myself to bitter criticism, I regard the memoirs of a Geoffroy Saint-Hilaire, a Wolf, or a Kowalevsky as having contributed much more to the progress of science than the anatomy of the cat by Straus-Durckheim, or that of the tortoise by Bojanus.

We shall endeavour to show what enormous influence the external conditions of existence may have upon the form of an animal, what astonishing resemblances may result from the action of identical causes upon originally different organisms. It will be the eternal glory of Lamarck that he was the first to

\* *Nablioudenia nade rajvetierne Brachiopoda*. Moscow, 1874, p. 34, note.

bring into the light this power of ethology. It will be the glory of Darwin that he has shown how much this action of the surrounding media is increased by natural selection, the idea of which is essentially inseparable from that of adaptation, selection at a given moment being determined by the limits of this adaptation.

We shall see hereafter how, in the particular instance of the Chatognatha and in some other interesting cases, pure adaptive analogies have been taken for relations of affinity. Without pretending to give a complete solution of these questions, which are too complex to be treated lightly, we shall esteem ourselves fortunate if we have indicated the nature of certain difficulties, and thus contributed to clear the road which our successors will have to traverse.

### *Convergence of Types by Pelagic Life.*

In a previous memoir\* I have dwelt upon the convergence of types by parasitism, and pointed out that this mode of existence gradually brought about in the most diverse animals organic modifications so profound as to cause the disappearance not only of the characters of orders and classes, but even of those of the great divisions or subkingdoms. Without the clue furnished by embryogeny we might easily be led to create families and genera including animals belonging to groups so distinct as the Trematoda, the Nudibranchiate Mollusca, the Cirripedes, and the Isopod and Copepod Crustacea. Since then, during the Scientific Congress at Lille, I have had the extreme satisfaction of learning that these opinions were shared by one of the most distinguished embryogenists of our time, Professor Carl Vogt. This eminent philosophical zoologist, without any knowledge of the memoir to which I have alluded, enunciated the same proposition, supporting it by precisely the same examples (*Sacculina*, *Entoconcha*, *Redice*).

Opinions of the same nature have also been expressed by Professor Martins (of Montpellier), one of the few French naturalists who have been able to understand the modern specific movement in the biological sciences. He says†:—"I cannot refrain from observing that the appearance of the same morphological type (of the same animal, so to speak) at various grades in the scale, is another argument in favour of community of origin combined with subsequent modifications. The

\* *Revue Scientifique*, July 11, 1874, 4<sup>e</sup> année, 2<sup>e</sup> série, no. 2, pp. 32 & 33.

† See C. Martins, 'La Création du monde organisé d'après les naturalistes de la nouvelle Ecole,' p. 15.

type of the monkey with hands and with a prehensile tail appears first of all in the chameleon—a reptile which does not creep but climbs, and twists its tail round the branch that bears it. This type reappears among the marsupials in the phalangers and opossums, among the rodents in the couendous (*Synetheres*), and among the plantigrade carnivores in the kinkajou (*Cercoleptes*), to become multiplied, diversified, and terminated in the prehensile-tailed monkeys of South America, such as the sapajous, howling monkeys, and spider monkeys. The flying dragon, among reptiles, is the first appearance of an animal which sustains itself in the air by means of a membrane stretched upon the sides of the trunk. The flying phalanger or *Petaurista* among marsupials, the flying squirrel among the rodents, and, lastly, the *Galeopithecus* or flying lemur are repetitions of the same morphological type from the reptiles up to the primates. . . . . In the gradual evolution of living creatures, notwithstanding profound differences of organization, the same media and the same needs have induced the development of the same forms, which heredity has fixed and maintained by the reproduction of the species.”

It will be seen that the learned Professor takes especially as examples organic arrangements relating to vital peculiarities of secondary rank. Thus we may say that some animals, such as the chameleon, the opossum, &c., present the same *ethological* type, rather than the same morphological type in the true sense of the word. It is the same with other animals with still more superficial resemblances due to direct mimetism, and not to parallelism of vital conditions\*. The action of surrounding media is of course exerted from the exterior towards the interior, and does not succeed in modifying the morphological type in creatures which are already strongly differentiated until after a very long time, and only with the aid of very imperious physiological necessities. As a matter of course, however, these physiological necessities are powerless of themselves to induce the convergence of types; and whilst we render all justice to our immortal Lamarck, we must not lose sight of the part played by natural selection in the preservation of the forms which are best adapted to a definite *ensemble* of external conditions.

One of the most energetic factors of this convergence is certainly, as has already been said, parasitism, and especially parasitism in its most absolute form—that is to say, that which

\* See, for more details upon the resemblances due to mimetism, my ‘*Recherches sur les Synascidies*,’ pp. 58 *et seqq.* The interesting investigations of Wallace and of some other zoologists are far from having exhausted this subject, which for many reasons deserves to be investigated afresh.

is combined with the permanent fixation and complete dependence of the parasite with relation to the affected organism. Parasitism in this sense produces results such that the zoologist, furnished only with the resources of anatomy and pure morphology, could never have referred certain animals to their true place in the classification.

But there are other groups of ethological conditions which, without acting in so remarkable a manner, nevertheless induce very interesting typical convergences, especially when they affect simple or feebly differentiated organisms. We shall pay attention at present only to pelagic life, and seek to determine with precision what are the modifications that this mode of existence may induce in the animals of various classes that are subjected to it. This will enable us to appreciate the value of the reasons which have led zoologists to place *Sagitta* in one group or another of the animal kingdom.

Pelagic animals are those which live in the open sea, generally near the surface of the water, and rarely approach the shore, upon which, however, they are sometimes cast by the winds. We find animals leading such an existence throughout the whole zoological series, from the Protozoa to the Vertebrata. If we leave out of consideration superficial currents and climatal zones, these animals live under very uniform and at the same time very special conditions, the action of which must impress upon the organism certain peculiar features, which may succeed in masking the morphological type, especially in the Invertebrata.

The characters of adaptation proper to pelagic life are:—

1. An extreme transparency of all the tissues, which renders the animal completely invisible, and enables it to escape easily from its enemies. This transparency exists in animals belonging to the most diverse groups. We observe it in the *Noctiluca*, the Siphonophora, the Medusæ, the Ctenophora, the Heteropod and Pteropod Mollusca, the *Salpæ* and *Pyrosomata*; in *Sagitta*, *Tomopteris*, and *Alciopæ*; and, lastly, in the *Leptocephali* among fishes.

2. The considerable development of certain organs of the senses, which often constitute the sole visible points of the animal. In general it is the eyes that present an enormous development with relation to the rest of the organization, as may be observed in a great number of the examples just cited; sometimes also the auditory apparatus, as in the Medusæ and the *Appendiculariæ*, and in *Mysis*, in which this apparatus is situated upon the caudal laminae.

3. A reduction of the digestive tube, which becomes considerable, although without being so marked as in parasitic

animals. Not to mention the numerous examples of this reduction that may be found among the Medusæ and Ctenophora, we meet in other groups with an atrophy of the digestive organs which may even reach complete disappearance absolutely, as in the Rhizostomes. This is what occurs, for example, in the curious genus *Monstrilla*, one of the pelagic Copepod Crustacea; the nucleus of the *Salpæ* and *Appendiculariæ* also represents a perfectly rudimentary state of the digestive tube of the Tunicata, if it be compared with the intestinal mass of the animals of that group which lead a sedentary life (Ascidia). The same may be said of the digestive tube of *Carinaria*, *Firoloides*, *Atlanta*, &c., when compared with that of the ordinary Gasteropoda. Finally, the *Sagittæ* also present an excessively reduced digestive tube, which occupies only a small portion of the length of the body.

This reduction of the digestive system in pelagic animals is evidently in relation with the precarious existence of these creatures, which are constantly pursued by numerous enemies. A voluminous stomach would impede their progress, which is generally very rapid, and would diminish the transparency which protects them.

4. A considerable development of the organs of generation and great fecundity. Here again it is sufficient, in order to ascertain this fact, to compare in the same group the pelagic animals with those which live attached. In *Appendicularia*, for example, the genital mass is much more voluminous than in the Ascidia, taking the proportion of this mass to the total volume of the body of the animal. This excessive multiplication of the pelagic animals must be attributed to the numerous chances of destruction to which creatures so badly protected are exposed, just as in the case of the parasites, among which the same fact is also observed.

5. A great number of pelagic animals present the phenomenon of phosphorescence, such as the *Noctiluçæ*, many Medusæ, the *Pyrosomata*, and *Phyllirhoë bucephala*. This phosphorescence, which is manifested especially when the animals are excited or alarmed, no doubt acts as a protection, and stops the pursuit of some enemies\*. I have not remarked that the *Sagittæ* are endowed with any such means of defence, which, moreover, is far from being peculiar to pelagic animals.

6. As an ethological character frequently observable in pelagic animals, we must cite social life: we know what

\* Pançeri and De Quatrefages have made the very interesting observation that phosphorescence is under the control of the nervous system.

numerous bands are almost always formed by the *Noctiluca*, Medusæ, Ctenophora, *Sagittæ*, Copepod Crustacea, *Mysides*, Pteropod Mollusca, &c.

It is evidently the resemblances of adaptation that *Sagitta* presents to *Amphioxus*, to the Heteropoda, and to *Tomopteris* and other Annelida, that have determined zoologists to place the Chætognatha sometimes among the Vertebrata, and sometimes with the Vermes, at a time when neither their anatomy nor their embryogeny was sufficiently known.

The arrangement of the nervous system evidently removes all possibility of an immediate approximation of *Sagitta* and the Vertebrata. Leydig and Kowalevsky have justly indicated that the nervous system resembles that of the Mollusca. It may also be compared to that of the Annelida; and in this there is nothing surprising, from what we now know of the close relationship (demonstrated by embryogeny) between the group of Annelida and that of Mollusca (Brachiopoda, Chitons, *Dentalia*, &c.).

On the other hand, this same nervous system removes the *Sagittæ* from the true Nematoids; and their attempted approximation to *Chaetosoma* does not appear to be completely justified by what we know of the organization of the latter.

The presence of chitinous setæ is another character in common with the Annelides; and indeed, from the anatomical point of view, the only serious argument that we can oppose to those who would unite the *Sagittæ* with ringed worms is the absence in the former of any metameral structure, even in the embryo. This character, on the other hand, approximates the Chætognatha to the phylum of the Mollusca, or, in a more general way, to the ancient animals from which have been derived on the one hand the Mollusca and on the other the Annelida. The presence of the vibratile disk and of the lateral invaginations also reminds us of the arrangement observable in groups allied to those inferior types of which we are speaking—for example, in the Rotifera or in the embryos of certain Annelids.

The very peculiar embryogeny of *Sagitta* (formation of a secondary general cavity), however, does not allow of our placing them directly among either the Mollusca or the Annelida. It is, in fact, a dilated embryogeny (without the formation, either primitive or secondary, of a nutritive vitellus) which is the indication of high antiquity of the type. It may, however, be the case that the development of the Annelides, which is not sufficiently known, represents the condensed form (with nutritive vitellus) of the evolution of the Chætognatha.

Thus it seems to us advisable to leave the *Sagitta* in a special group, which, under the name of Chætognatha, must take its place at the base of the phylum of the Annelida, of which this group represents a divergent branch adapted for a pelagic existence.

Other examples will show still better the practical importance that may attach to speculative considerations such as those which we have expounded with regard to the convergence of types by pelagic life.

The illustrious Von Baer, in a memoir dated last year, has endeavoured to demonstrate that the *Ascidia* and the *Salpæ* are Mollusca presenting the same typical structure as the Heteropoda; but the smallest acquaintance with the development of these animals suffices to prove, as we have endeavoured to do elsewhere, that the resemblance between a *Biphora* and a *Firoloides* is a result of adaptation, and that the analogies of the Tunicata with the Gasteropoda are no more real than those which have been attempted to be established between the same animals and the Lamellibranchiata\*.

Forbes thought he could find great affinities between the larvæ of the *Ascidia* and the *Hydroida*. On the other hand, Carl Vogt formerly placed the *Ctenophora* among the Molluscoida. An English naturalist, Macdonald, taking up a few years ago these ancient ideas, gave the following classification of the Molluscoida:—

#### MOLLUSCOIDA.

Intestine separated from the cavity of the body.	$\left\{ \begin{array}{l} \text{Curvature primitively hæmal,} \\ \text{finally neural . . . . .} \\ \text{Curvature simply neural . . . .} \end{array} \right.$	$\left. \begin{array}{l} \textit{Ascidiozoa.} \\ \textit{Brachiopoda} \\ \textit{and Polyzoa.} \end{array} \right\}$
Intestine straight and communicating with the cavity of the body . . . . .		

Macdonald regards the *Ctenophora* as a central type, from which are derived on the one hand, by progression, the Molluscoida, on the other, by degradation, the Hydrozoa. This curious classification also has evidently for its starting-point false homologies due to adaptation, which have appeared to the author of more importance than the fundamental differences presented by the embryogeny of these animals. The comparison of the pelagic types (natatory Tunicata, *Ctenophora*, and *Hydroida*) is evidently the starting-point of these lucubrations, which look as if they were a century old, and nevertheless were published in 1864.

\* See Giard, "Embryogénie des Ascidiés, et l'origine des Vertébrés," *Revue Scientifique*, 4<sup>e</sup> année, No. 2, July 11, 1874.



Under other circumstances adaptation to pelagic life causes certain adult animals to resemble embryonic forms of other animals belonging to higher types, or produces apparent analogies between larval forms pertaining to different groups. In his fine work on the *Metamorphoses of Man and Animals* (1862), M. de Quatrefages, speaking of the *Amphioxus*, says:—“It is allowable to ask ourselves whether this animal, which is placed in the lowest rank of Vertebrates, and which in many respects approaches the Annelida Errantia, is really a perfect animal. In some parts of its organization it reminds us of the *Ammocetes* of our brooks. May it not be the larva of *Petromyzon marinus* or of some other species?” In 1867, in a memoir upon this singular vertebrate, M. Bert insisted on the facts which show that it is an adult creature; and in the same year Kowalevsky gave a complete embryogeny of it. Nevertheless in 1871, at the Academy of Boston, in presence of Louis Agassiz, the question whether *Amphioxus* is not the larva of a Myxinoid fish was discussed over again\*.

We have several times observed, in the neighbourhood of Boulogne, troops of young *Clupeæ* of astonishing transparency, and resembling the *Leptocephali* in general aspect. Now it is well known that zoologists have not yet completely solved the question whether these *Leptocephali* are or are not adult forms. Gill and several other ichthyologists assert that they are embryonic forms; Peters, on the contrary, affirms † that they cannot be regarded as the embryos of the *Cepolæ* or of other fishes. According to Gill, *Leptocephalus Morrisii* is the young of *Conger vulgaris*, *Hyopropurus messinensis* belongs to *Nettastoma melanura*, and *Stomasunculus* is the larva of a Clupeoid ‡.

If such questions are difficult to solve in the case of animals so high as the fishes, it will easily be understood how much greater are the difficulties met with by the zoologist when he tries to establish the true homologies which may exist between the larvæ of the lower animals.

It seems to me that one of the most important and necessary investigations for the progress of embryogeny would be to distinguish what is due to heredity and what is the result of adaptation to pelagic life in embryonic forms, such as the larvæ of the Echinoderms, the *Pilidium* of the Nemertians, the *Actinotrochæ*, *Mitrariæ*, *Cyphonautes*, certain larvæ of Planariæ,

\* Similar difficulties occurred formerly with regard to *Phyllosoma*, *Cuma*, &c.

† Monatsb. Akad. Wiss. Berlin, 1864, p. 399.

‡ Proc. Acad. Nat. Sci. Philad. 1864.

Annelides, &c. Upon organisms still so slightly differentiated external conditions act in a very energetic manner; and their action is multiplied by heredity in creatures with a free and dilated embryogeny. We must therefore keep watch against the apparent homologies which often mask real but yet only slightly marked differences of organization—"When we have to do with the starting-point of an angle, no modification in the divergence of the lines is indifferent."

Among those who will read the preceding pages there are some who will regard such researches as rash, as useless theories, or as facile dissertations; so great is even still the infatuation of certain naturalists for the exaggerations of the Cuvierian school, and for the ideal and artistic morphology of some of his successors. We have nothing to urge against those who persist, in contempt of embryogenic data, in seeking in adult forms for supposed homologies of connexion and an arbitrary plan determined beforehand. One cannot discuss matters with a partisan. To those who pretend that it is *easy* to reason upon known facts, and who prefer to seek and store up in their memoirs histological details and observations in descriptive anatomy, we say with Professor Hæckel:—"Whoever has good eyes and a microscope, assiduity, and patience may now-a-days acquire a certain notoriety by microscopical discoveries, but without therefore deserving the name of a naturalist. This title must be reserved for the man who endeavours not only to see the particular facts, but also to grasp their ethological bond."

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#### IX.—*Observations on the Genus Platycrinus.*

By Fort-Major THOMAS AUSTIN, F.G.S.

HAVING for a long time remarked the anomaly of retaining in the genus *Platycrinus* those species which deviate from the typical character in having the mouth, or anal orifice, or whatever the office the aperture may have been intended to perform, placed *laterally* or nearly so, whereas the typical species and some others have the *centre* of the ventral dome elevated into a tube from one to two inches in height, it is therefore proposed to remove those species with *excentric* apertures into a new genus, retaining *Platycrinus levis* and all those with *proboscidiiform central* tubes in the original genus.